for Ruffed Grouse (Bump et al. 1947). Conversely, in another subspecies of the Willow Ptarmigan, there was greater chick survival during population increases than during decreases (Bergerud 1970).

Although the juvenile/adult ratio was not significantly correlated with the preceding spring's population level in Sage Grouse, that ratio was positively correlated with the following spring's population level. This situation suggests that juvenile mortality over the summer period is more variable than over the winter. Constant mortality over winter has been reported for both Willow Ptarmigan (Bergerud 1970, Myrberget 1972) and Rock Ptarmigan (Weeden and Theberge 1972).

The effect of relatively great August precipitation on the proportion of juveniles in the fall harvest in this study was striking. Yearly precipitation reaches its low point in southern Idaho in July (0.35 ± 0.35 cm, c.v. = 100%) which is a relatively sharp drop from that in June (1.17 ± 1.03 cm). August precipitation (0.54 ± 0.80 cm, c.v. = 148%) is substantially more variable than that in July. Thus, young birds may be especially susceptible to effects of August precipitation if they are stressed by having just passed through the driest month of the year. The availability of forbs and insects for food undoubtedly varies directly with precipitation. Summer mortality among juveniles may also be largely responsible for declines of Ruffed Grouse and Sharp-tailed Grouse (Keith 1963). It is puzzling, however, that years with no August precipitation may also result in a relatively large proportion of juvenile Sage Grouse in the harvest and that July precipitation was negatively correlated with the juvenile/adult ratio. I have assumed that the number of adults remains more constant over summer than the number of juveniles and that the juvenile/adult ratio is mainly a function of variability in juvenile production and survival. Obviously, adult numbers also vary and the relationship between summer precipitation and survival of both age classes deserves further study.

Although my work did not involve any assessment of the possible effects of predation, information is available for southern Idaho and northern Utah that bears directly on this question. Lack (1954) believed that predator-prey interactions could produce cyclical population fluctuations under certain conditions, especially where there were few alternate prey species for a given predator. If the main prey species was cycling for some reason (e. g., Keith 1983) and began a decline, predators would switch to alternate prey. Because the predator populations had increased with their main prey, they would be at high enough densities to cause a decline in the alternate prey populations, and, thus, a cycle might be induced. If this were the case, oscillations in the alternate prey populations should have a lag of one or two years following oscillations of the main prey (Lack 1954).

In southern Idaho and northern Utah such a predator-prey system involves the black-tailed jackrabbit (Lepus californicus) as main prey species, coyote (Canis latrans) as main predator (Wagner and Stoddart 1972, Gross et al. 1974, Stoddart 1978, unpubl.), and Sage Grouse as one possible alternate prey species. Jackrabbit populations in the Curlew Valley of northern Utah apparently have had a 10-year cycle since at least 1963 (Fig. 8). This region corresponds with the Utah lek complexes of this paper. Jackrabbit data from the Idaho National Engineering Laboratory (INEL) is closely synchronized with that from Curlew Valley (Fig. 8). Although the INEL data is available for a shorter time period, it suggests that a similar cyclicity is occurring in southern Idaho. Other independent data from southern Idaho support those in Fig. 8. Jackrabbit population peaks have occurred in 1919-1922, 1927, 1936, 1942, 1952, 1958-1960, 1970-1971, and 1981 (J. Harris, pers. comm.).

Stoddart (1978) concluded that the observed jackrabbit cycle in Curlew Valley could be largely accounted for by coyote predation. Given the sharp decline in jackrabbit densities following peaks in 1971 and 1981 (Fig. 8) coyotes would proabably have switched to alternate prey. If Sage Grouse were affected by this system one would expect Sage Grouse populations to have begun declining in 1972 and 1982. Clearly, this was not the case. Sage Grouse populations in all three states peaked at least one year before jackrabbit populations in every instance. Keith (1963) reported that snowshoe hare (Lepus americanus) populations also peak slightly later than grouse, and Hoffman (1958), after reviewing many studies, found that grouse declines frequently precede hare declines. Thus, there is no support for the predator-prey system as outlined by Lack (1954) having induced cycles in Sage Grouse populations. However, the striking synchrony of jackrabbit and Sage Grouse populations in Idaho and Utah certainly calls for explanation. It is not unlikely that predation does play an important role, but the dynamics have yet to be discovered.

The importance of the recognition of a possible 10-year cycle in Sage Grouse lies both in the field of management and research. Evaluations of grouse population responses to habitat changes are critically dependent on understanding the long-term population dynamics of the species, especially where such evaluations may be done over a period of only a few years. In addition, Sage Grouse habitat is often delimited based on the number, size, and locations of leks. Obviously, the years in which leks are located and counted are important. Ten years data may be required to even begin an adequate definition of just the breeding habitat of a population.

The tetraonids as a whole exhibit several behavioral and ecological features that make them attractive subjects for population studies (Bendell 1972b), and I believe the lekking species are even more suitable than the territorial species. In particular, the yearly congregation of male and female Sage Grouse on traditional leks affords several advantages: 1) although the variability in numbers of birds attending a given lek daily in a particular year may be substantial, the major factors influencing attendance are fairly well understood (Jenni and Hartzler 1978). Therefore, lek counts are probably good indicators of population size and trend; 2) the birds are tolerant of vehicles near the lek making not only counts but the study of behavior, which may be important to understanding cycles in grouse (Robel 1972), relatively easy; 3) large blocks of relatively uniform habitat are accessible by vehicle at most times of the year; 4) many lek sites are already documented by wildlife and land management agencies; 5) a large amount of historical data on both Sage Grouse and their habitat, especially wildfire and grazing, is available. Thus, Sage Grouse may be one of the best vertebrate species yet for long-term population studies. This is an especially intriguing situation because black-tailed jackrabbit and coyote populations are also apparently cycling in the same geographic region and much is already known of the dynamics of this predator-prey system.

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LITERATURE CITED

Autenrieth, R. E. 1981. Sage Grouse management in Idaho. Boise, Idaho, Idaho Department of Fish and Game.

Bendell, J. F. 1972a. Population dynamics and ecology of the Tetraonidae. Proc. Intern. Ornithol. Congr. 15:81-89.

-----. 1972b. Concluding remarks on the tetraonid symposium. Proc. Intern. Ornithol. Congr. 15:170-177.

Bergerud, A. T. 1970. Population Dynamics of the Willow Ptarmigan *Lagopus lagopus alleni* L. in Newfoundland 1955 to 1965. Oikos 21:299-325.

-----. 1971. The past abundance of Willow Ptarmigan on the Avalon Penninsula of Newfoundland. Can. Field-Nat. 84:21-23.

Bulmer, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. J. Anim. Ecol. 43:701-718.

Bump, G., R. W. Darrow, F. C. Edminster, & W. F. Crissey. 1947. The Ruffed Grouse. Life history, propagation, management. Buffalo, New York, N. Y. State Cons. Dept.

Cole, L. C., 1951. Population cycles and random oscillations. J. Wildl. Manage. 15:233-252.

-----. 1954. Some features of random population cycles. J. Wildl. Manage.

18:2-24.

Dasmann, R. F. 1964. Wildlife biology. New York, John Wiley & Sons, Inc.

Dixon, W. J. (Ed.). 1981. BMDP statistical software. Berkeley, California, Univ. California Press.

Finerty, J. P. 1980. The population ecology of cycles in small mammals/ Mathmatical theory and biological fact. New Haven, Yale Univ. Press.

Gross, J. E., L. C. Stoddart, & F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildl. Monogr. No. 40.

Gudmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. Proc. Intern. Ornithol. Congr. 12:259-265.

-----. 1972. Discussion on the tetraonid symposium. Proc. Intern. Ornithol. Congr. 15:179.

Hamerstrom, F., & F. Hamerstrom 1954. Population density and behavior in Wisconsin Prairie Chickens (Tympanuchus cupido pinnatus). Proc. Intern. Ornithol. Congr. 11:459-466.

----- & -----. 1961. Status and problems of North American grouse. Wilson Bull. 73:284-294.

Hildén, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53-75.

Hoffman, R. S. 1958. The role of predators in "cyclic" declines of grouse populations. J. Wildl. Manage. 22:317-319.

Jenkins, P., A. Watson, & G. R. Miller. 1967. Population fluctuations in the Red Grouse Lagopus lagopus scoticus. J. Anim. Ecol. 36:97-122.

Jenni, D. A., & J. E. Hartzler. 1978. Attendance at a Sage Grouse lek: implications for spring censuses. J. Wildl. Manage. 42:46-52.

Keith, L. B. 1963. Wildlife's ten-year cycle. Madison, Wisconsin, Univ. Wisconsin Press.

-----. 1983. Role of food in hare population cycles. Oikos 40:385-395.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous

United States. Amer. Geogr. Soc. Spec. Publ. 36.

Lack, D. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.

Leopold, A. 1933. Game management. New York, Charles Scribner's Sons.

Linden, H., & P. Rajala. 1981. Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. Finn. Game Res. 39:13-34.

Lords, J. L. 1951. Distribution, ecology and population dynamics of the Sage Grouse in Utah. Unpublished M.S. Thesis. Salt Lake City, Utah, Univ. Utah.

Myrberget, S. 1972. Fluctuations in a north Norwegian population of Willow Grouse. Proc. Intern. Ornithol. Congr. 15:107-120.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Denver, Colorado, Sage Books, Inc. and Wyo. Fish and Game Comm.

Potts, R. 1972. Discussion on the tetraonid symposium. Proc. Intern. Ornithol. Congr. 15:182.

Redfield, J. A. 1975. Comparative demography of increasing and stable populations of Blue Grouse (Dendragapus obscurus). Can. J. Zool. 53:1-11.

Robel, R. J. 1972. Possible function of the lek in regulating tetraonid populations. Proc. Intern. Ornithol. Congr. 15:121-133.

Rowan, W. 1948. The ten-year cycle: outstanding problem of Canadian conservation. Edmonton, Alberta, Dept. of Extension, Univ. Alberta.

Stoddart, L. C. 1978. Population dynamics, movements and home range of black-tailed jackrabbits (Lepus californicus) in Curlew Valley, northern Utah. Final Report U. S. Dept. Energy. Conract No. E11-1-1229.

Wagner, F. H., & L. C. Stoddart. 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. J. Wildl. Manage. 36:

329-342.

Wallestad, R. O. 1975. Life history and habitat requirements of Sage Grouse in central Montana. Helena, Montana, Montana Dept. Fish and Game.

Watson, A., & R. Moss. 1979. Population cycles in the Tetraonidae. Orn. Fenn. 56:87-109.

Weeden, R. B., & J. B. Theberge. 1972. The dynamics of a fluctuating population of Rock Ptarmigan in Alaska. Proc. Intern. Ornithol. Congr. 15:90-106.

Williams, G. R. 1954. Population fluctuations in some Northern Hemisphere game birds (Tetraonidae). J. Anim. Ecol. 23:1-34.

Winward, A. H. 1970. Taxonomic and ecological relationships of the big sagebrush Complex in Idaho. Unpublished Ph.D. Thesis. Moscow, Idaho, Univ. Idaho.

Table 1. Habitat and count information for the Sage Grouse lek complexes.

Lek Complex / Elevation / Habitat	Name of lek	Years of data	Number of Males: Mean	SD
Picabo Hills	Wedgetop[a]	30	28.8	29.8
1500 m	Sonner's Reservoir[a]	30	20.1	17.5
Artemisia	Fenced Field[a]	28	45.7	26.4
tridentata	Square Lake[a]	32	31.1	21.1
wyomingensis	Spudpatch[a]	28	77.9	60.1
	LI65	20	33.7	23.7
	LI77	21	51.8	32.0
	Buck Lake	27	25.7	18.1
	Ridge	9	55.9	44.4
Bennett Hills	Fir Grove[a]	24	36.1	25.2
1500 m	Johnson Well [a]	29	55.1	25.7
A. vaseyena	Willow Springs[a]	28	18.7	11.0
	Association Well	23	18.4	16.2
	Ben Dohr Reservoir	25	14.7	11.9
	Hill City Road[b]	17	16.5	10
North Laidlaw	Paddleford Flat[a]	19	27.7	12.1
1500 m	Rock Pile[a]	14	18.5	14.9
A. tripartita	Paddleford No. 1[a]	9	35.8	30.7
	Moran Lake [a]	15	15.9	13.8

Table 1. (Continued).

South Laidlaw	Shale Butte Cabin[a]	29	24.8	23.7
1400 m	Kimama Section 32[a]	30	21.5	17.7
A. t.	Laidlaw Airstrip[a]	31	19.6	13.7
wyomingensis	Steamboat Lake No. 1[a]	30	48.3	40.4
	Beartrap Airstrip	14	35.7	21.1
Dove Creek	Dove Creek	25	71.7	43.4
1700 m	Warm Springs Road	14	10.6	8.5
A. nova	Upper Dove Creek	13	25.9	14.6
Rosebud	Dry Basin	25	84.6	49.4
1750 m	Keg Springs	19	12.1	9.8
A. nova	Badger Flat[c]	21	28.2	16.9
Hardister Creek	Hardister Creek Road	15	34.4	19.5
1800 m	Meadow Creek Pass	14	16.7	6.8
A. arbuscula	Red Bank Springs	15	34.1	26.5
Wall Canyon	Nolan Ranch	8	110.4	31
1800 m	Nolan Sattelite Ground	7	24.4	19
A. arbuscula	Wall Canyon Seeding	8	24.8	20.6
Grass Valley	Clover Creek	9	28.0	14.5
1725 m	Cherry Ridge	9	12.8	6.9
A. arbuscula				

Table 1. (Continued)

Squaw Valley 1700 m *A. arbuscula*	Squaw Valley	7	42.6	17.8

[a]Idaho leks used in correlation and regression analysis.

[b]Habitat is *A. t. wyomingensis*.

[c]Lek was grouped somewhat arbitrarily with Rosebud.

Table 2. Significant correlations between the criterion variable, Lek_t, and predictor variables for Idaho data. Linear-regression equations are also given.

Lek Complex	$\underline{n}$	Predictor Variable	$\underline{r}$	$\underline{P}$[a]
All Combined	94	Lek_{t-1}	0.73	< 0.001
		$JanP_t$	0.22	< 0.05
		$MarP_{t-1}$	-0.22	< 0.05
		$FebP_t$	-0.21	< 0.05
$Lek_t = 7.5 + 0.7\ Lek_{t-1}$ ($\underline{r}^2 = 0.53$)				< 0.001
Picabo Hills	28	Lek_{t-1}	0.67	< 0.001
		$JunP_{t-1}$	0.43	< 0.05
		$JanP_{t-1}$	0.39	< 0.05
$Lek_t = 12.9 + 0.7\ Lek_{t-1}$ ($\underline{r}^2 = 0.45$)				< 0.001
South Laidlaw	28	Lek_{t-1}	0.75	< 0.001
		$JanP_t$	0.47	< 0.02
		$MarP_{t-1}$	-0.44	< 0.02
$Lek_t = 5.6 + 0.8\ Lek_{t-1}$ ($\underline{r}^2 = 0.56$)				< 0.001
Bennett Hills	24	$DecT_t$	0.57	< 0.005
		$DecP_t$	-0.51	< 0.02
(No variables entered into regression)				

Table 2. (Continued).

North Laidlaw	14	Lek_{t-1}	0.90	<0.001
$Lek_t = 1.8 + 0.8\ Lek_{t-1}$ ($\underline{r}^2 = 0.81$)				<0.001

[a]See Methods for interpretation of $\underline{P}$ values involving Lek_t and Lek_{t-1}.

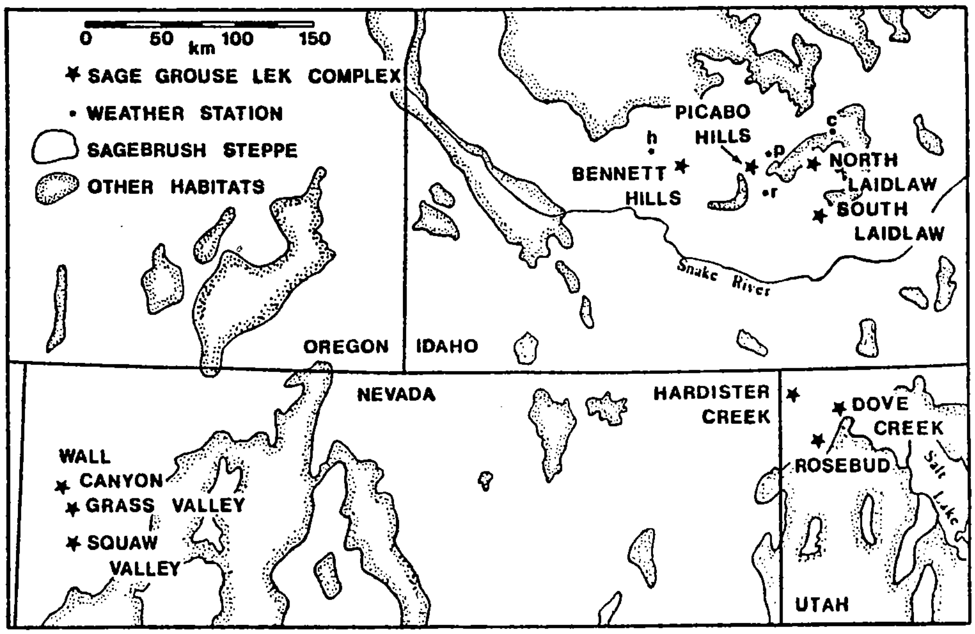

Fig. 1. Map of the Intermountain West showing location of lek complexes, the potential sagebrush steppe habitat (after Küchler 1964), and NOAA weather stations (h = Hill City, p = Picabo, r = Richfield, c = Craters of the Moon).

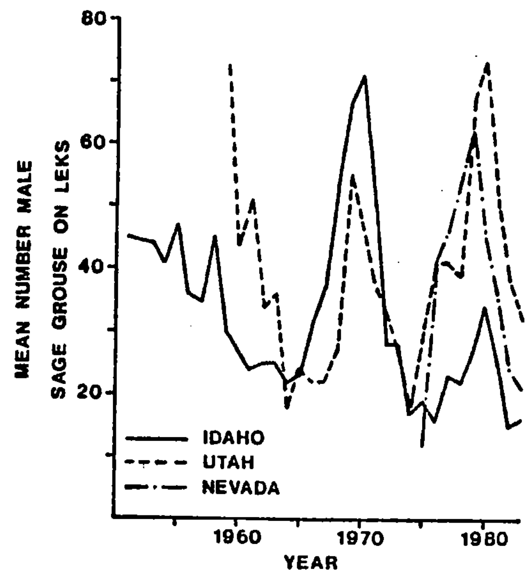

Fig. 2. The mean maximum number of male Sage Grouse per year on subject leks in Idaho, Utah, and Nevada.

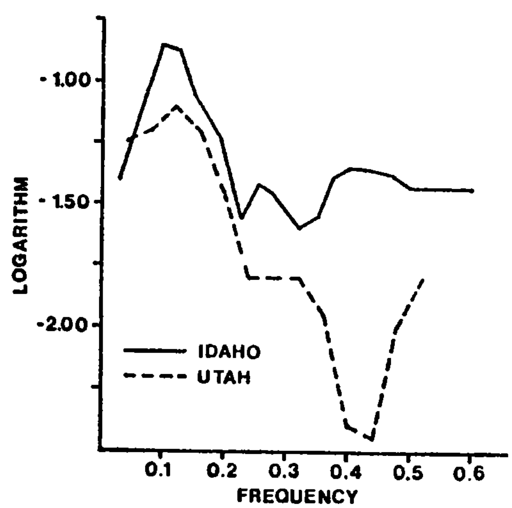

Fig. 3. Spectral analysis of mean lek counts for Idaho and Utah (see text).

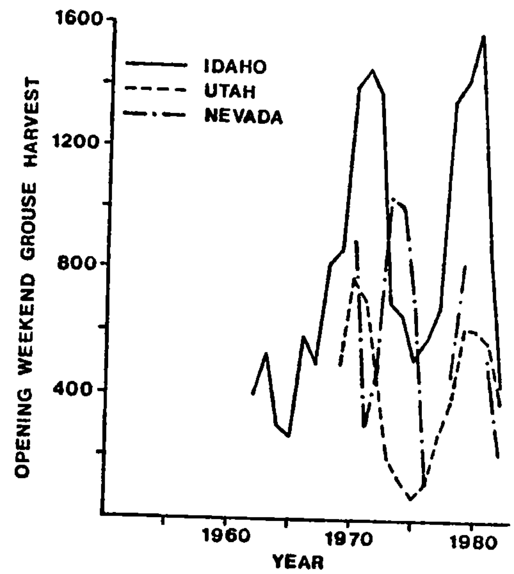

Fig. 4. The yearly harvest of Sage Grouse on the opening weekend of hunting season in Idaho, Utah, and Nevada from geographic regions that correspond with the lek complexes.

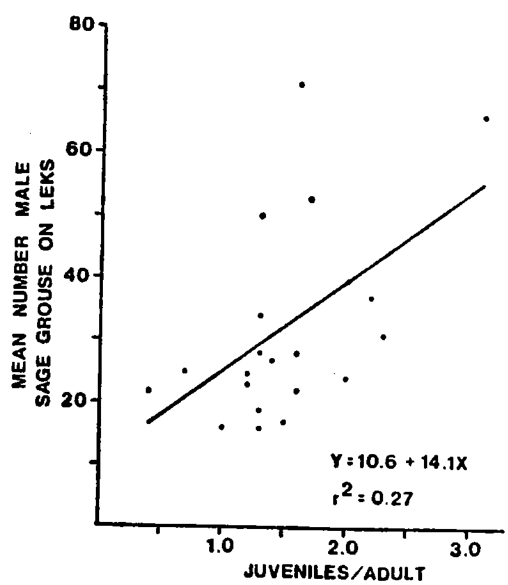

Fig. 5. The relationship between the juvenile/adult ratio of Sage Grouse in the harvest on the opening weekend of hunting season in Idaho and the mean maximum number of males on leks the following spring ($\underline{F} = 6.71$, $\underline{P} < 0.05$).

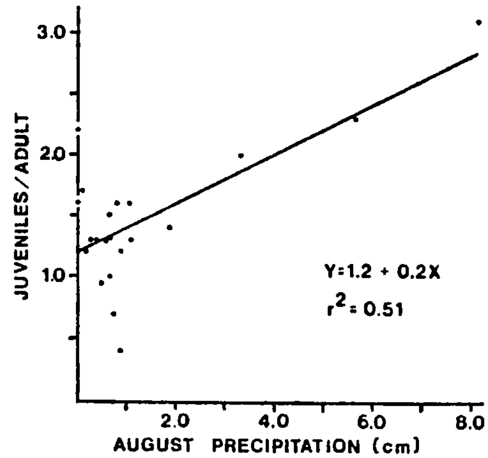

Fig. 6. The relationship between the juvenile/adult ratio in the harvest in Idaho and August precipitation of the same year (F = 19.82, $P < 0.001$).

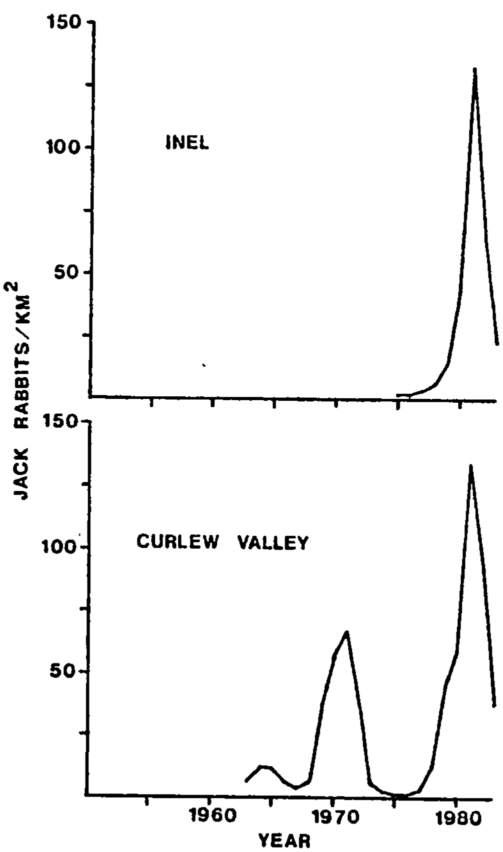

Fig. 7. Spring black-tailed jackrabbit densities in the Curlew Valley of northern Utah and Idaho National Engineering Laboratory (INEL) of southern Idaho (L. C. Stoddart, unpubl.).